BRYOPHYTES OF THE PEAT MAT AT PONKAPOAG POND, EASTERN MASSACHUSETTS, WITH TAXONOMIC AND ECOLOGICAL NOTES ON SPHAGNUM

WALTER S. JUDD

Ponkapoag bog is located in the town of Canton in Norfolk County, Massachusetts, and occupies a little over 100 acres along the northwest shore of Ponkapoag Pond. Along its northern boundary the bog (actually a poor fen) is separated from the surrounding oak-white pine forest by an abrupt slope. Several small streams flow into the bog mat from the north and northwest, and Ponkapoag Pond itself has an outlet at its southwest corner. The mat is in contact with the mineral substrate of the pond except at its extreme outer edge. The bog comprises several vegetation types including (1) Chamaedaphne calvculata thicket, (2) Chamaecyparis thyoides forest and (3) Acer rubrum swamp-forest. These vegetation types are not absolutely distinct and grade into each other. Chamaedaphne thickets are usually nearer the open water of the pond, while Acer rubrum swamp-forest is limited to the outer margin of the bog near the surrounding upland forest. Chamaecyparis trees have been removed from portions of the study area, and these places are now occupied by dense thickets of Chamaedaphne calvculata. Decodon verticillatus is abundant along the peaty shore of the pond (i.e., at the outer, unconsolidated edge of the mat nearest the pond). In each of the vegetation types occur several distinct bryophyte communities. These are discussed below, with special emphasis on Sphagnum, of which 15 species have been found within the study area. Dominant vascular plants of the Chamaedaphne thickets include Chamaedaphne calvculata, Kalmia angustifolia, Myrica gale, Vaccinium macrocarpon, and the herbs Drosera intermedia, D. rotundifolia, Sarracenia purpurea, Peltrandra virginica, Eriophorum virginicum, Rhynchospora alba, and Carex spp.¹ The surface beneath these thickets is a series of hummocks, hollows, and mats of Sphagnum. The most abundant species include the ombrotrophic to

¹Here, as throughout, the nomenclature of vascular plants follows M. L. Fernald (1950), except for *Xyris* which follows R. Kral (1966).

563

564

[Vol. 82

only weakly minerotrophic Sphagnum capillifolium, S. flavicomans, S. papillosum, and S. magellanicum, which are not found in the more mineral-rich Acer rubrum swamp-forest (see table 1). Sphagnum cuspidatum and S. torrevanum are also common, and S. recurvum s. stricto is an occasional member of the community. Dicranum scoparium and Aulacomnium palustre sometimes occupy hummock tops, and lower on the hummock sides the Sphagna may be mixed with Drepanocladus uncinatus or D. fluitans. On disturbed and/or eroded hummocks, Mylia anomala, Cladopodiella fluitans, Cephalozia connivens, or Aulacomnium palustre are often found. The species of Sphagnum occurring in these hummocks and hollows can be arranged in a series in relation to their position above (or below) the water level (see Figure 1). Sphagnum torrevanum always occurs in the deepest portions of pools, while S. cuspidatum is found in shallow pools and depressions, around the margins of deeper pools, or in low mats. Sphagnum recurvum can occur in hollows (but only rarely under water) or in low mounds around clumps of vegetation (base of shrubs, trees, etc.). Sphagnum papillosum and S. magellanicum occur at slightly higher levels and characteristically form dense mats or low to moderately high (i.e., to 30 cm.) hummocks. The highest portions of the hummocks (i.e., to

Table 1: The distribution of species of Sphagnum occurring at Ponkapoag Bog. (Note: **** = abundant, *** = common, ** = locally common, * = occasional, + rare, 0 = not present).

Species	Chamaedaphne thicket	Chamaecyparis forest	Acer rubrum forest
S. papillosum	****	**	0
S. magellanicum	***	**	0
S. palustre	0	+	****
S. henryense	0	+	***
S. imbricatum	0	0	****
S. recurvum	*	****	**
S. fallax	0	+	***
S. cuspidatum	**	**	**
S. torrevanum	**	**	**
S. fimbriatum	+	****	****
S. girgensohnii	0	0	+
S. capillifolium	****	**	0
S. russowii	0	0	+
S. flavicomans	***	**	0
S. squarrosum	0	0	*

1980] Judd — Bryophytes 565

ca. 60 cm.) are occupied by Sphagnum flavicomans and/or S. capillifolium. However, both species are sometimes rather variable in position, and occasionaly occupy low flat mats with S. papillosum or S. magellanicum. Similar zonations of species have been reported by Andrus (1974), Moss (1953), Ratcliffe and Walker (1958), Rose (1953), Spearing (1972), Vitt, Crum, and Snider (1975); and Vitt and Slack (1975). The vertical zonation of species probably results from the galacturonic acid content (and thus cationexchange capacity) of individual species and their differential ability to hold (and conduct) water. Cladopodiella fluitans, Cephalozia connivens and Mylia anomala are common in low depressions and around small pools in rather low, open thickets of Chamaedaphne calyculata, Kalmia angustifolia, and Vaccinium macrocarpon (with various sedges, Drosera spp., and Xyris difformis). They are often mixed with Sphagnum cuspidatum and S. papillosum.

Chamaecyparis thyoides forest can be quite open and sunny with many shrubs such as Vaccinium corymbosum, Kalmia angustifolia, Chamaedaphne calyculata, Rhododendron viscosum, Pyrus (Aronia) arbutifolia, Ilex verticillata, and Nemopanthus mucronata, or quite dense with little other than closely spaced Chamaecyparis trees. A distinctive assemblage of species including Tetraphis pellucida, Microlepidozia sylvatica, Cephalozia connivens, Dicranum flagellare, Mylia anomala, and Odontoschisma denudatum occurs on rotted, decorticated cedar stumps (and logs). Humus at the bases of such stumps (or on living trees) is often covered with Sphagnum fimbriatum (especially at densely shaded sites), Mylia anomala, Cephalozia connivens, C. macrostachya, or Drepanocladus fluitans. Sphagnum recurvum and S. cuspidatum often occur in depressions between hummocks, and S. torrevanum is found in the deepest pools. Sphagnum recurvum becomes dominant in more open portions of Chamaecvparis forest and reaches its greatest abundance in this vegetation type. In these areas it forms low to slightly raised mats between the various trees and shrubs and forms small hummocks around their bases. It is often mixed with S. papillosum, S. magellanicum, and S. fimbriatum. Other common bryophytes at the bases of trees and shrubs in these areas are Dicranum flagellare, D. scoparium, Tetraphis pellucida, and Hypnum pallescens (all usually well above water-level), along with Cephalozia spp., Aulacomnium palustre, and Drepanocladus flui-

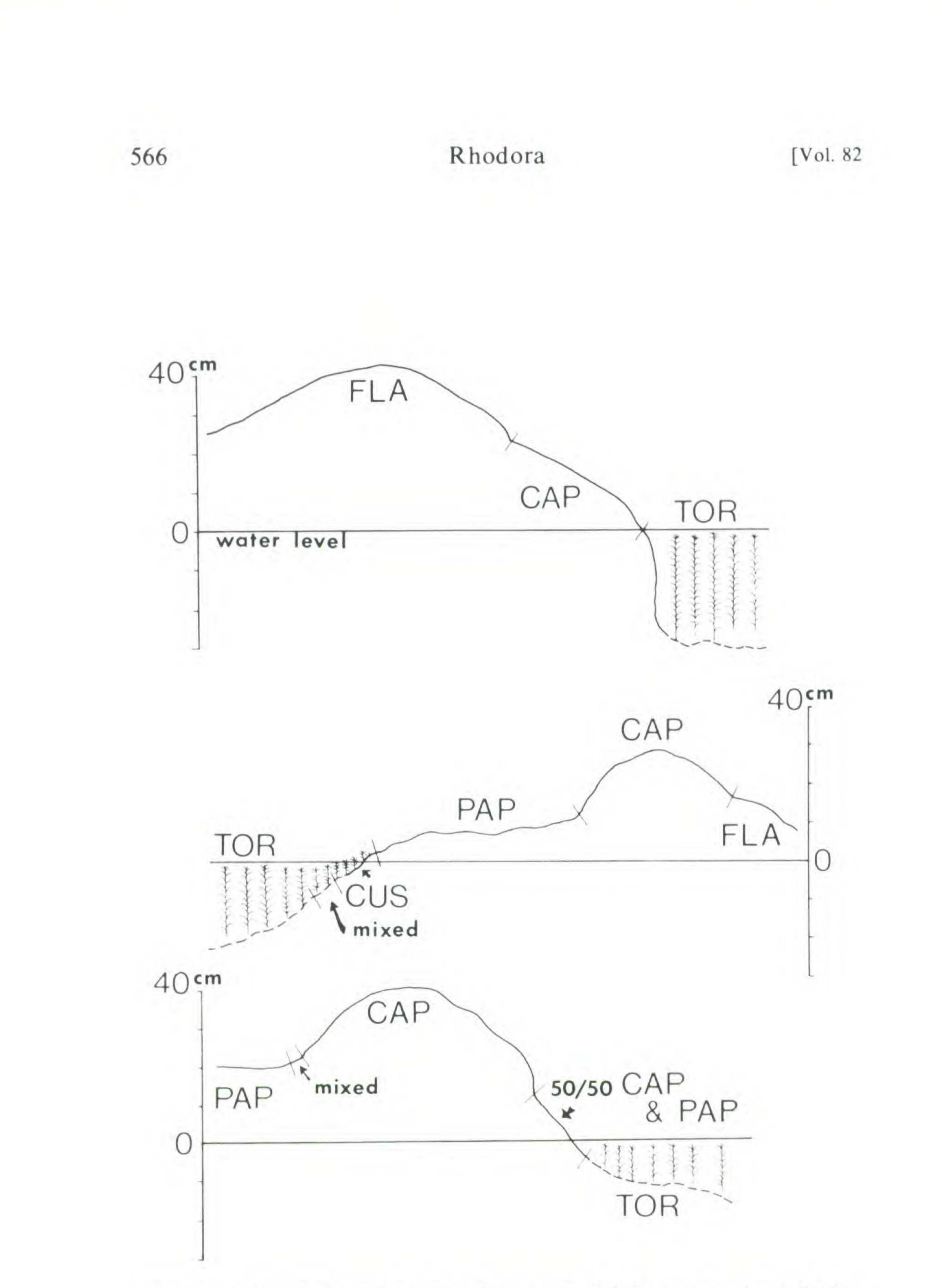


Figure 1.: Selected hummock-hollow diagrams of *Sphagnum* species at Ponkapoag Bog. Scale shows height above (or below) water level (in 10 cm units). CAP =*Sphagnum capillifolium*; CUS = S. *cuspidatum*; FLA = S. *flavicomans*; PAP = S. *papillosum*; TOR = S. *torreyanum*.

Judd — Bryophytes 567

tans (found near water-level or mixed with above). Pallavicinia lyellii is often found over organic material in open areas of the Chamaecyparis forest.

The swamp-forest at the periphery of much of the bog is composed of scattered Acer rubrum trees with a dense undergrowth of various ericaceous shrubs (e.g., Vaccinium corymbosum, Leucothoë racemosa, Kalmia angustifolia, Rhododendron viscosum, and Lyonia ligustrina) with Clethra alnifolia, Ilex verticillata, Pyrus arbutifolia, Viburnum recognitum, Nemopanthus mucronata, Rosa palustris, and Cephalanthus occidentalis. Moist, decorticated logs and stumps in this forest are characteristically covered with Cephalozia spp., Nowellia curvifolia, Dicranum flagellare, Odontoschisma denudatum, Callicladium haldanianum, Lophocolea heterophylla, Tetraphis pellucida, and Aulacomnium palustre. Species of Sphagnum (e.g., S. palustre, S. imbricatum, S. henryense, S. fimbriatum, etc.) often become established on the wettest of the logs, and eventually completely cover them to form Sphagnum hummocks. Leucobryum glaucum is often present along with Dicranum flagellare on dry logs.

Sphagnum hummocks are frequent at the bases of shrubs, trees, and ferns, and are usually composed of the minerotrophic S. imbricatum, S. palustre, S. henryense (all essentially limited to the Acer rubrum forest), and S. fimbriatum. Unlike in the open Chamaedaphne thicket or Chamaecyparis forest, Sphagnum does not form a continuous covering over the peat. Sphagnum squarrosum and S. fallax are occasionally also present, and two rare species (S. russowii and S. girgensohnii) are limited to this habitat (Table 1). Sphagnum cuspidatum and S. torreyanum also occur but are restricted to small ephemeral or permanent pools. Drepanocladus fluitans, D. aduncus var. polycarpus, Leptodictyum riparium, and Calliergon cordifolium are common on twigs, organic debris, and at the base of Decodon clumps or other shrubs, in low, open, often inundated areas of the Acer rubrum swamp. Drepanocladus fluitans (with Aulacomnium palustre) is also usually

present in the lower portions of the organic hummocks around the bases of trees and shrubs.

Platygyrium repens and *Dicranum flagellare* occur as epiphytes on the higher portions (i.e., above ca. 0.5 m.) of tree trunks. Near the base of such trees at the margin of the *Acer rubrum* swampforest nearest the upland forest, several other species occur, such as

[Vol. 82

Plagiothecium denticulatum, Mnium cuspidatum, M. hornum, Thuidium delicatulum, Tetraphis pellucida, Hypnum pallescens, and Leucobryum glaucum. Plagiothecium laetum and P. latebricola are found only at the base of trees in the drier portions of the Acer rubrum woods adjacent to the surrounding upland forest. Bryhnia novae-angliae occurs on humus in a few shaded areas along a small ditch which flows into the Acer rubrum swamp-forest.

568

The occurrence of such a high number of Sphagnum species in the bog (see table 1) is probably related at least in part to the diversity of suitable microhabitats which are arranged along both vertical (hummock to hollow, see Figure 1) and horizontal (ombrotrophic to minerotrophic) environmental gradients. No other genus present in the bog (with the possible exception of *Carex*) has as many species and the diversity of habitats as does Sphagnum.

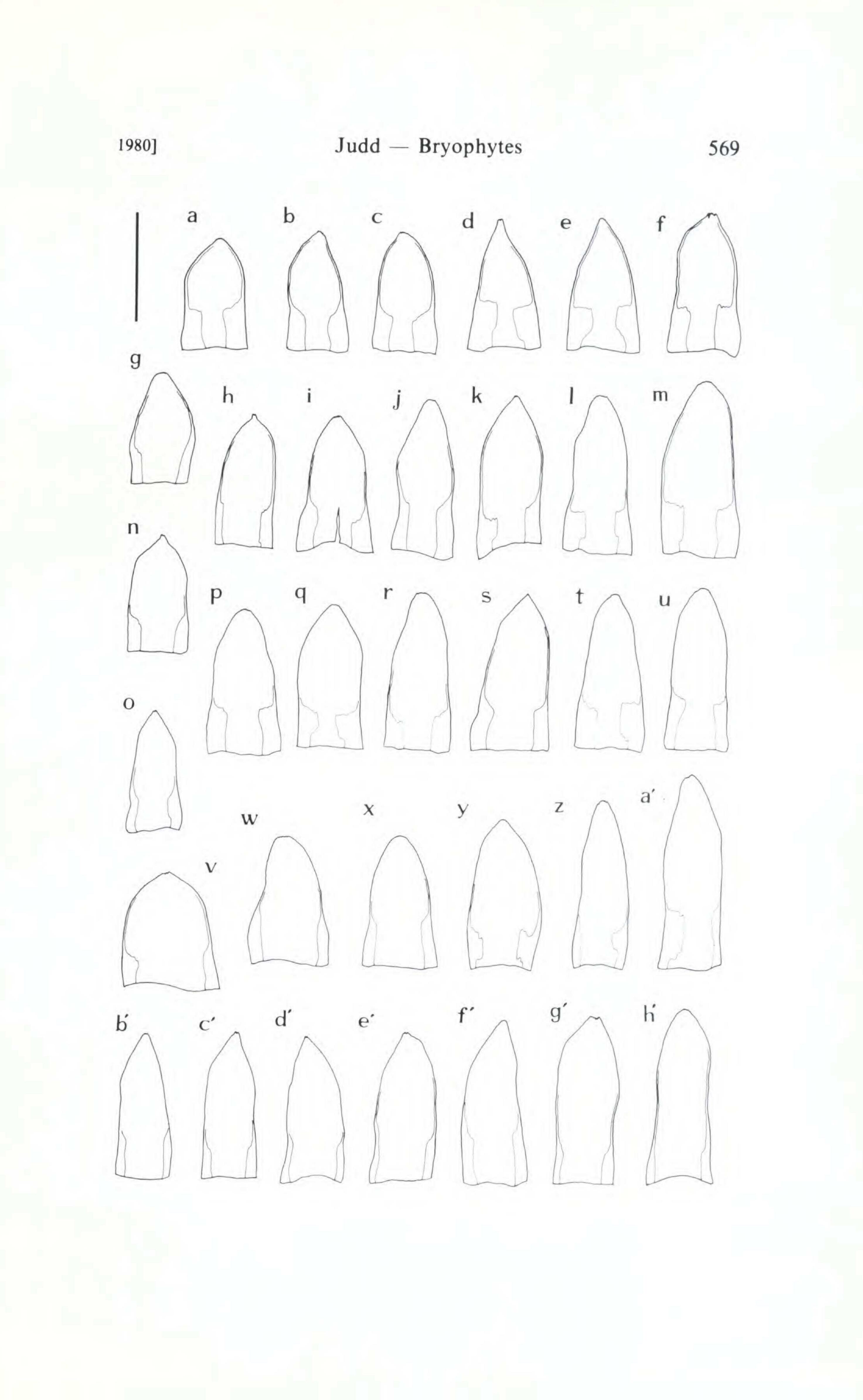
THE BRYOPHYTE FLORA

Although the area surveyed is small, the several distinct habitats present support an interesting bryophyte flora of 60 species (i.e., 44 mosses and 16 liverworts). The catalog which follows is based almost exclusively on my own collections (made between September 1975 and July 1978), and unless otherwise indicated all the collection numbers are my own. A set of voucher specimens is deposited in the Farlow Herbarium. The families are listed in phylogenetic order and follow Crum, Steere, and Anderson (1973) for the mosses and Stotler and Crandall-Stotler (1977) for the liverworts. The occurrence of each species in the vegetation zones of the bog is indicated by a code in parentheses following the collection numbers. The zone in which the species is most frequent is listed first. These zones are:

(A.) Acer rubrum swamp-forest (Cc.) Chamaecyparis thyoides forest (Cd.) Chamaedaphne calyculata thicket

Figure 2: Variation in stem leaf shape and marginal linear cell development in Sphagnum capillifolium from Ponkapoag Bog. Bar equals 1 mm.

Collection numbers: a, 2136; b,c, 1947; d,e, 1960; f, 1020; g, 1927, top of hummock; h, 1974; i, 1949; j,k, 1943; 1, 1978; m, 1961; n, 1949; o, 1954; p, 1973; q, 1999; r, 1977; s, 1916, bottom of hummock; t, 1977; u, 1978; v-x, 967; y, 1915, bottom of hummock; z, 1977; a', 1978; b', 1949; c'1927, bottom of hummock; d'. 1915, top of hummock; e', 1872; f', 1961; g',h', 1927, bottom of hummock.



Rhodora [Vol. 82 570

The distribution of the 15 species of Sphagnum occurring within the study area was especially interesting and is summarized in Table 1 and Figure 1.

MUSCI

SPHAGNACEAE

Sphagnum capillifolium (Weiss) Schrank — 967, 999, 1020, 1022, 1061, 1872, 1913, 1915, 1916, 1921, 1927, 1928, 1931, 1943, 1944, 1947, 1949, 1954, 1960-1962, 1973-1982, 1993-1999, 2101, 2136. (Cd, Cc). This morphologically variable taxon often has been divided into several species (see Andrus, 1974, 1976), and if these segregates are recognized, then the Ponkapoag material falls chiefly within Sphagnum rubellum Wils. and S. subtile (Russow) Warnst. According to Andrus (1974) S. rubellum is characterized by its lingulate to lingulate-triangular stem leaves with a strong border (moderately broadened basally) and with 1-3-septate and often fibrillose cells. The branch leaves are 5-ranked. The capitulum varies from flat-topped to slightly rounded and often has a 5-parted, stellate appearance. In contrast, S. subtile is characterized by its triangular-lingulate to lingulate stem leaves with a very strong border (greatly broadened basally) and with smaller 1(2)-septate and usually efibrillose cells. The branch leaves are 5-ranked in coastal forms (but not 5-ranked inland) and the capitulum is flat-topped but not stellate in appearance. However I was not able to separate the Ponkapoag material into two discrete groups by using the above characters. The variation in shape of the stem leaves and the development of their marginal linear cells form a continuum (see Figure 2) among specimens collected at Ponkapoag Bog. Continuous variation was also observed in cells of the stem leaves, which vary from fibrillose to efibrillose and from 0-1-septate to 1-3-septate (see Figure 3). Also the branch leaves vary from clearly 5-ranked to imbricate and the capitula vary from flat-topped and clearly star-shaped to hemispherical. Some plants were found (e.g., 1961, 1960, 967) with certain characters of S. subtile and other characters of S. rubellum. Much of this variation may be due to hydrologic stress and other environmental factors. For example, small plants with imbricate branch leaves and nearly hemispherical capitula are more common near the tops of hummocks than in the hollows between them. However some variation is probably genetically controlled because certain populations had consistently

Judd — Bryophytes 571

more clearly 5-ranked branch-leaves, or developed consistently smaller and more strongly bordered stem-leaves than other populations. It is noteworthy that mixed populations (e.g., 1995) of deep red and pinkish-brown individuals also occur. At least until the factors resulting in the above described patterns of variation are better understood it seems best to delimit *S. capillifolium* in the

broad sense (see Andrews, 1913; Crum, 1976; Hill, 1976; and comments of Nyholm, 1954, concerning genetically determined but intergrading variation patterns within this species).

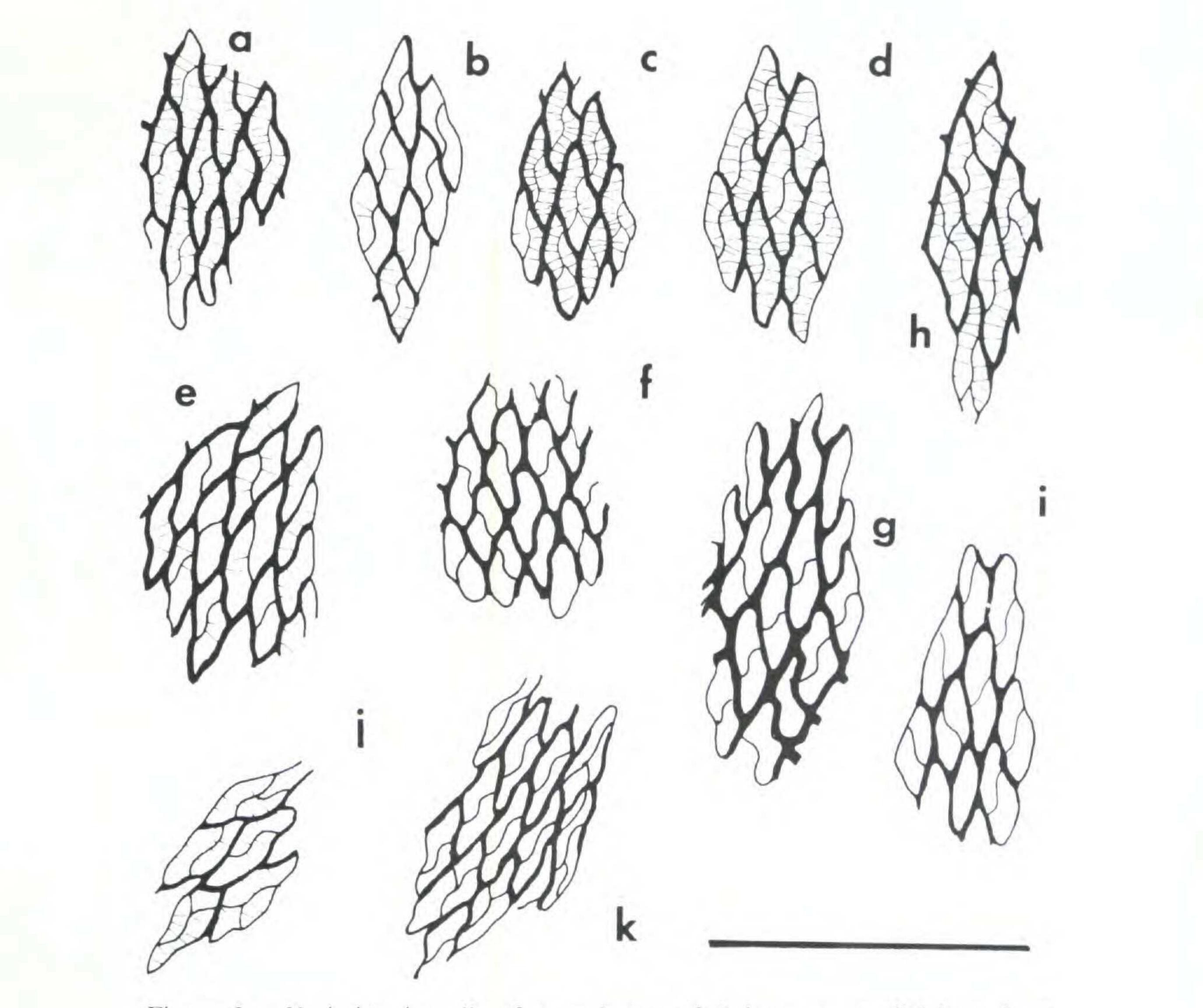


Figure 3.: Variation in cells of stem leaves of *Sphagnum capillifolium* from Ponkapoag Bog. Cells projected and traced from mid-portion of each leaf; bar equals 0.25 mm.

Collection numbers: a, 1916, bottom of hummock; b, 1947; c, 1916, top of hummock; d, 1943; e, 1020; f, 2136; g, 967; h, 1872; i, 1949; j, 1927; k, 999.

572 [Vol. 82

- S. cuspidatum Ehrh. ex Hoffm. 890, 964a, 1649, 2113, 2114. (Cd, Cc, A).
- S. fallax (Klinggr.) Klinggr. 1021, 1652, 1950, 2108. (A, Cc). This species is separated from the closely related Sphagnum recurvum by its smaller size, apiculate stem leaves and slightly exposed to slightly enclosed chlorophyllose cells of the branch leaves (as seen in transverse section); (see Andrus, 1974; Nyholm, 1954; Smith, 1977).
- S. fimbriatum Wils. ex J. D. Hook. & Wils. 841, 844, 891, 895, 964b, 1002, 1019, 1621, 1651, 1910, 1917, 1956, 2104-2107. (A, Cc, Cd).
- S. flavicomans (Card.) Warnst. 1010, 1011, 1871, 1872, 1914, 1919, 1928, 1931, 1948, 2096-2100. (Cd, Cc).

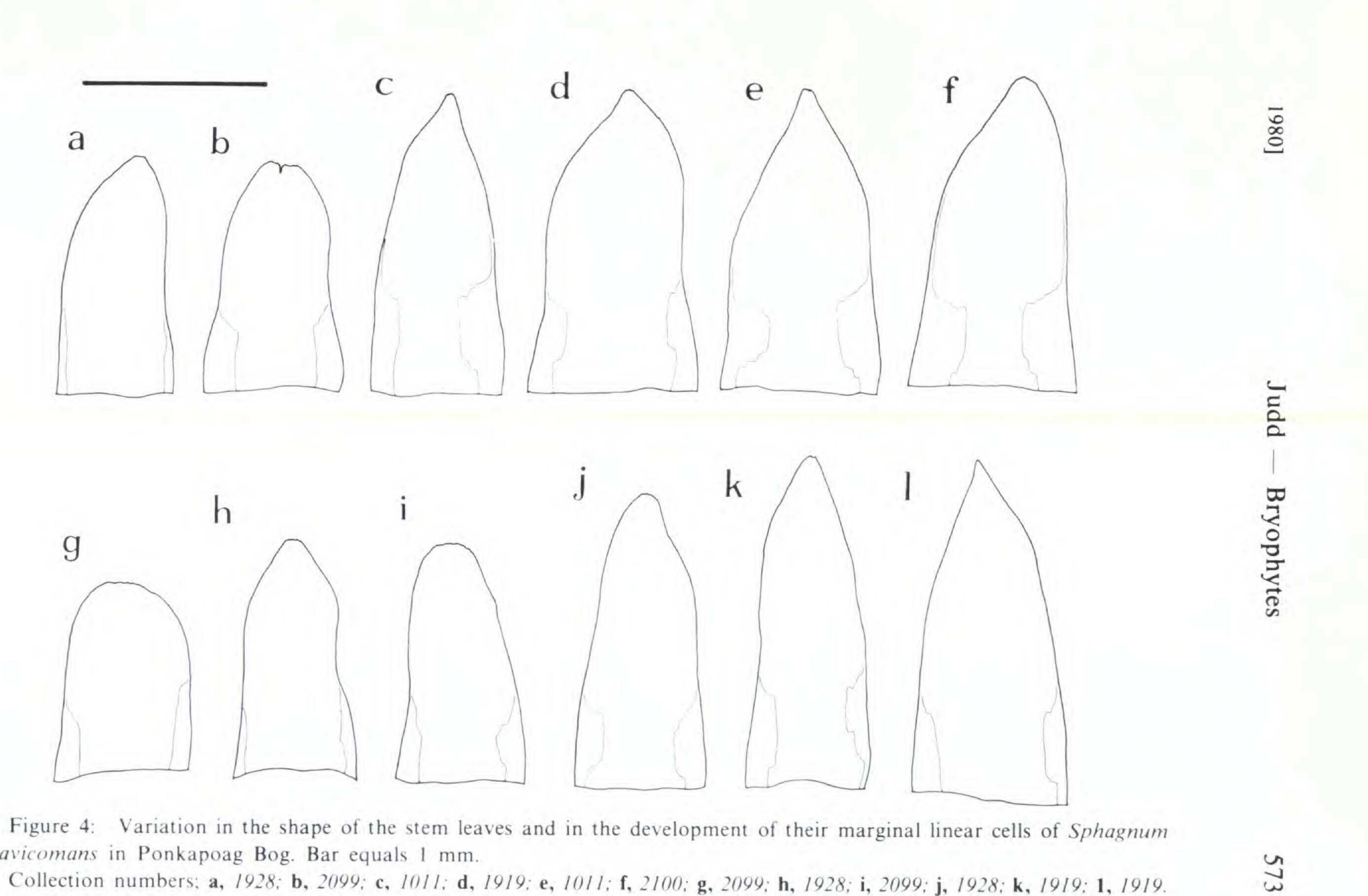
This species is usually easily separated from *Sphagnum capil-lifolium*, with which it is often found intermixed, by its usually larger size, orange-brown color (i.e., stems yellowish-green to brown and *not* purplish-red pigmented), nearly always imbricate branch leaves, and often larger stem leaves with cells nearly always l-septate (Figure 4). However, poorly-pigmented,

- young forms may be difficult to identify.
- S. girgensohnii Russow 2103. (A).
- S. henryense Warnst. 1879, 1881, 1911, 1912, 2129, 2133. (A, Cc).
- S. imbricatum Russow 892, 1014, 1016, 1017, 1957, 2131, 2135. (A).
- S. magellanicum Brid. 897, 909, 1009, 1873. (Cd, Cc).
- S. palustre L. 888, 889, 1878, 1880, 1908, 1909, 1951, 2130, 2132, 2134. (A, Cc).
- S. papillosum Lindb. 843, 846, 851, 899, 908, 1015, 1875-1877, 1945, 2118-2128. (Cd, Cc).
- S. recurvum P.-Beauv. s. stricto 845, 849, 893, 896, 898, 1000, 1001, 1922-

1926, 1929, 1930, 1946, 2109-2112. (Cc, A, Cd).

This species is separated from *S. fallax* by having often erose to fimbriate (apex more or less rounded) stem leaves, chloro-phyllose cells of the branch leaves included in transverse section, and a larger size.

S. russowii Warnst. — 1003. (A).



flavicomans in Ponkapoag Bog. Bar equals 1 mm.

Collection numbers; a, 1928; b, 2099; c, 1011; d, 1919; e, 1011; f, 2100; g, 2099; h, 1928; i, 2099; j, 1928; k, 1919; 1, 1919.

[Vol. 82

S. squarrosum Crome — 842, 1018. (A).

S. torreyanum Sull. - 900, 1036-1038, 1874, 2115-2117. (Cd, Cc, A).

DICRANACEAE

Dicranum flagellare Hedw. - 833, 836, 881, 887, 894, 904, 2137. (A, Cc).

D. scoparium Hedw. — 837, 903, 954, 996 (Cc, Cd).

LEUCOBRYACEAE

Leucobryum glaucum (Hed.) Aongstr. ex Fr. - 953, 961 (A. Cc). BRYACEAE Pohlia nutans (Hedw.) Lindb. — 859. (A). MNIACEAE Mnium cuspidatum Hedw. - 1041. (A).

M. hornum Hedw. 1054a, 1054b, s.n., 12 July 1976. (A).

M. punctatum Hedw. var. elatum Schimp. — s.n., 12 July 1976. (A).

AULACOMNIACEAE

Aulacomnium palustre (Hedw.) Schwaegr. - 839, 848, 856, 884, 944. 949, 971, 1057 (A, Cc, Cd).

CLIMACIACEAE

Climacium americanum Brid. — 917, 976, 978, 1024. (A).

THUIDIACEAE

Helodium paludosum (Sull.) Aust. - 920, 1055. (A). Thuidium delicatulum (Hedw.) BSG. — 1048. (A).

AMBLYSTEGIACEAE

Calliergon cordifolium (Hedw.) Kindb. — 857, 1647, 1650. (A, Cc). Campylium radicale (P.-Beauv.) Grout — 997. (A).

1980] Judd — Bryophytes 575

Drepanocladus aduncus (Hedw.) Warnst. var. polycarpus (Bland. ex Voit) Roth — 973. (A).

D. fluitans (Hedw.) Warnst — 854, 906, 1648. (A, Cc, Cd).
D. uncinatus (Hedw.) Warnst. — 960, 1952. (Cd, Cc).
Leptodictyum riparium (Hedw.) Warnst. — 858, 972, 1058, 1654, s.n., 7

July 1976. (A, Cc).

BRACHYTHEACEAE

Bryhnia novae-angliae (Sull. & Lesq. ex Sull.) Grout — s.n., 12 July 1976. (A).

PLAGIOTHECIACEAE

Plagiothecium denticulatum (Hedw.) BSG. – 1052. (A),

- P. laetum BSG. 1043. (A).
- **P. latebricola** BSG. 1050. (A).

HYPNACEAE

Callicladium haldanianum (Grev.) Crum — 885, 918, 965, 975, 1059. (A, Cc).

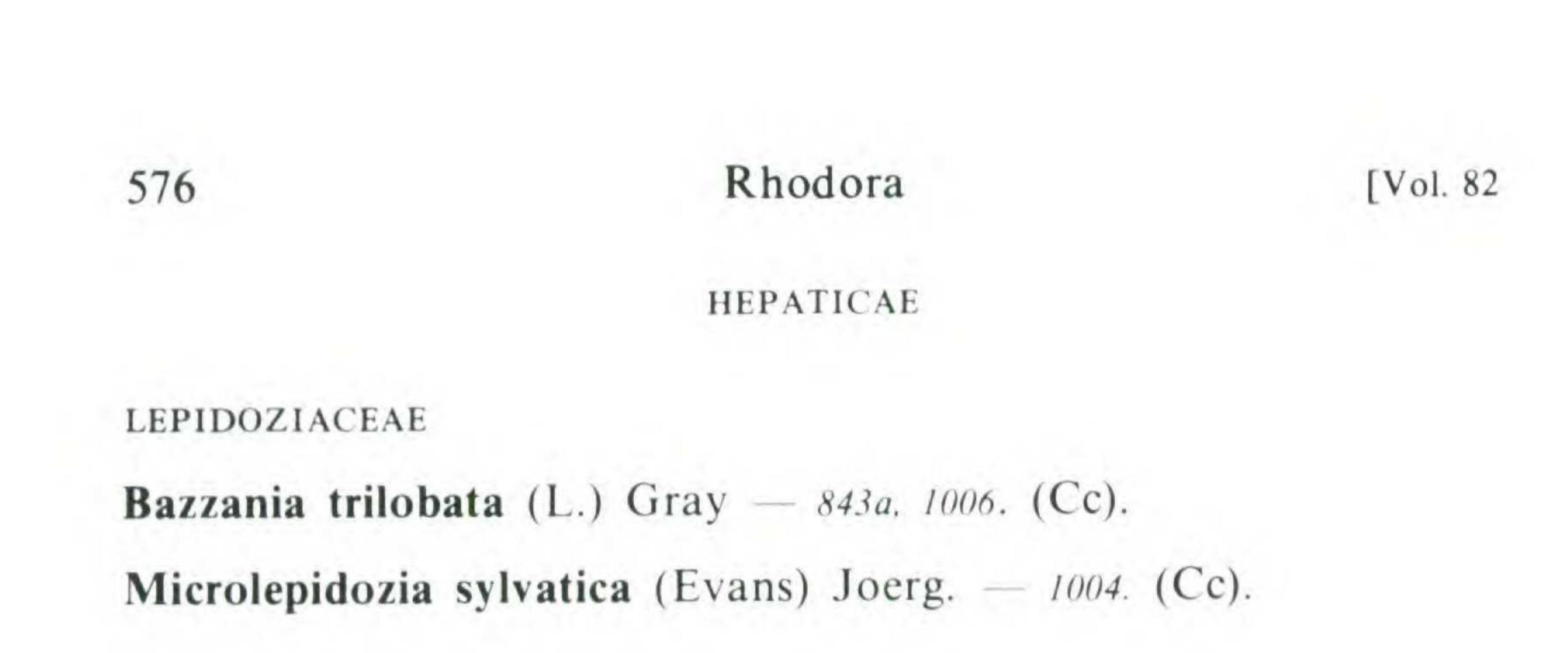
Herzogiella turfaceae (Lindb.) Iwats. — 835. (A).
Hypnum cupressiforme Hedw. — 1653. (A).
H. lindbergii Mitt. — 853. 860a, 883, 901, 1060. (A, Cc).
H. pallescens (Hedw.) P.-Beauv. — 880, 1053. (A).
Platygyrium repens (Brid.) BSG — 1051. (A).

TETRAPHIDACEAE

Tetraphis pellucida Hedw. — 850, 855, 886, 2138. (A, Cc).

POLYTRICHACEAE

Atrichum angustatum (Brid.) BSG. - 1047. (A).



CALYPOGEJACEAE

Calypogeja muelleriana (Schiffn.) K. Müller — 834, 840. (Cc, A).
C. sphagnicola (Arn & Perss.) Warnst. & Loeske — N. G. Miller 8068. (Cd).

CEPHALOZIACEAE

Cephalozia catenulata (Hüb.) Lindb. — 951a, 951b. (A).

C. connivens (Dicks.) Spruce — 955, 963, 1013. (Cd, Cc).

C. macrostachya Kaal. – 948, 1958, s.n., October 1975. (Cc).

Cladopodiella fluitans (Nees) Buch — 907, 1012a, 1012b, 1918, 2139.

(Cd).

Nowellia curvifolia (Dicks.) Mitt. – 905. (A).

ADELANTHACEAE

Odontoschisma denudatum (Mart.) Dumort. — 1005, 1039. (A, Cc). O. prostratum (Sw.) Trevis. — 1041. (A).

CEPHALOZIELLACEAE

Cephaloziella elachista (Jack) Schiffn. - 840b. (Cc).

LOPHOCOLEACEAE

Lophocolea heterophylla (Schrad.) Dumort. - 952, 998, 1045. (A).

JUNGERMANNIACEAE

Mylia anomala (Hook.) Gray — 852, 902, 905, 947, 962, 1955. (Cc, Cd).

1980] Judd — Bryophytes 577

PALLAVICINIACEAE

Pallavicinia lyellii (Lindenberg) Gray — 847, 945, 946 (A, Cc, Cd).

PELLIACEAE

Pellia epiphylla (L.) Corda — 977, 1046. (A).

ACKNOWLEDGMENTS

I wish to thank Dr. Norton G. Miller for his encouragement during the course of the project and for his helpful suggestions concerning the manuscript.

LITERATURE CITED

ANDREWS, A. L. 1913. Sphagnaceae. North American Flora 15: 3-31.
ANDRUS, R. E. 1974. The Sphagna of New York State. Ph.D. Dissertation, State University of New York, College of Environmental Science and Forestry, Syracuse, New York. 421 pp.
ANDRUS, R. E. 1976. Three neglected Sphagnum species of the section Acutifolia.

- p. 16. American Bryological and Lichenological Society. Abstracts of contributed papers presented at the annual meeting. New Orleans, La.
 CRUM, H. A. 1976. Mosses of the Great Lakes Forest. Revised Ed. University of
 - Michigan, Ann Arbor, Michigan. 404 pp.
- CRUM, H.A., W. C. STEERE, & L. E. ANDERSON. 1973. A new list of mosses of North America north of Mexico. Bryologist 76: 85-130.
- FERNALD, M. L. 1950. Gray's Manual of Botany, ed. 8. American Book Co., New York.
- HILL, M. O. 1976. A critical assessment of the distinction between Sphagnum capillaceum (Weiss) Schrank and S. rubellum Wils. in Britain. Jour. Bryol. 9: 185–191.
- KRAL, R. 1966. Xyris (Xyridaceae) of the continental United States and Canada. Sida 2: 177-260.
- Moss, E. H. 1953. Marsh and bog vegetation in northwestern Alberta. Canad. J. Bot. 31: 448-470.
- NYHOLM, E. 1954. Illustrated moss flora of Fennoscandia, vol. 2. Musci. CWK

Gleerup/Lund, Sweden. 799 pp.

- RATCLIFFE, D. A., & D. WALKER. 1958. The Silver Flowe, Galloway, Scotland. Jour. Ecol. 46: 407-445.
- ROSE, F. 1953. A survey of the ecology of British lowland bogs. Proc. Linn. Soc. London 164: 186-211.

SмITH, G. L. 1977. Sphagnum recurvum. Phytologia 36: 171-176.

[Vol. 82

SPEARING, A. M. 1972. Caton-exchange capacity and galacturonic acid content of several species of *Sphagnum* in Sandy Ridge Bog, central New York State. Bryologist 75: 154–158.

- STOTLER, R. & B. CRANDALL-STOTLER. 1977. A checklist of the liverworts and hornworts of North America. Bryologist 80: 405 428.
- VITT, D. H., H. CRUM, & J. A. SNIDER. 1975. The vertical zonation of *Sphagnum* species in hummock-hollow complexes in northern Michigan. Mich. Bot. 14: 190–200.

VITT, D. H., & N. G. SLACK. 1975. An analysis of the vegetation of *Sphagnum*dominated kettle-hole bogs in relation to environmental gradients. Canad. J. Bot. 53: 332-359.

DEPARTMENT OF BOTANY UNIVERSITY OF FLORIDA GAINESVILLE, FLORIDA 32611

578